A New Genus of Cryptodiran Turtles (Testudinoidea, Chelydridae) From the Upper Cretaceous Hell Creek Formation of Montana

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ABSTRACT

Emarginachelys cretacea is described as a new genus and species of cryptodiran turtle and is placed in the Chelydridae on the basis of shared derived characters. The holotype is a nearly complete skeleton from the Hell Creek Formation (Maestrichtian) of Montana. *Emarginachelys* is the oldest known member of the superfamily Testudinoidea as defined by Gaffney (1975a). The Chelydridae are hypothesized to be a monophyletic group, sharing a cruciform plastron ligamentously attached to the carapace, a reduced entoplastron, long costiform processes on the nuchal bone, an elongate jugal, and the pectineal processes of the pubis not strongly divergent. *Emarginachelys* is hypothesized to be the most primitive genus of the Chelydridae since it does not have the derived characters shared by advanced chelydrids. Advanced chelydrids have the frontal bones separated from the orbital rim, a premaxillary "hook," constriction of the otic bridge, a closed incisura columella auris, a serrated carapacial margin, and peripheral fontanelles.

INTRODUCTION

The turtle superfamily Testudinoidea includes the majority of living turtles, both in numbers and diversity. As defined by Gaffney (1975a), the testudinoids include the pond turtles (Emydinae and Batagurinae), the tortoises (Testudininae), and the snapping turtles (Chelydridae). Previously, the oldest known definitive testudinoids were a

chelydrid, *Protochelydra zangerli*, from the Paleocene of North Dakota (Erickson, 1973), and a pond turtle, *Ptychogaster* sp., from the Paleocene of the Big Horn Basin in Wyoming (Estes, 1975). The family Chelydridae has a sparse fossil record in Tertiary deposits of North America and Europe, and only two species are extant, both restricted to the New World (Fig. 1). Gaffney (1975b) includes the Recent Asiatic genus *Platysternon* in the Chelydridae, but I do not consider this to be a parsimonious interpretation of the affinities of this genus (see discussion below).

Fig. 1. Generalized distribution of recent chelydrid turtles. Star shows location from which the holotype of *Emarginachelys* was recovered.

The species described herein as *Emarginachelys cretacea* n. gen. et sp. is the oldest and most primitive species placed in the Chelydridae. A University of Kansas field party (Don and Stan Rasmussen and John Chorn) collected the holotype in 1971 from the Upper Cretaceous Hell Creek Formation in Montana. The type specimen is a nearly complete skeleton, still mainly articulated when found. Fossil turtles of this quality are extremely rare, especially in Mesozoic strata.

The turtle was preserved as a large "clast" in a medium grained sandstone which lies 5.2 m. (27 feet) below the "Z" coal of the Paleocene Ft. Union Formation (Fig. 2).
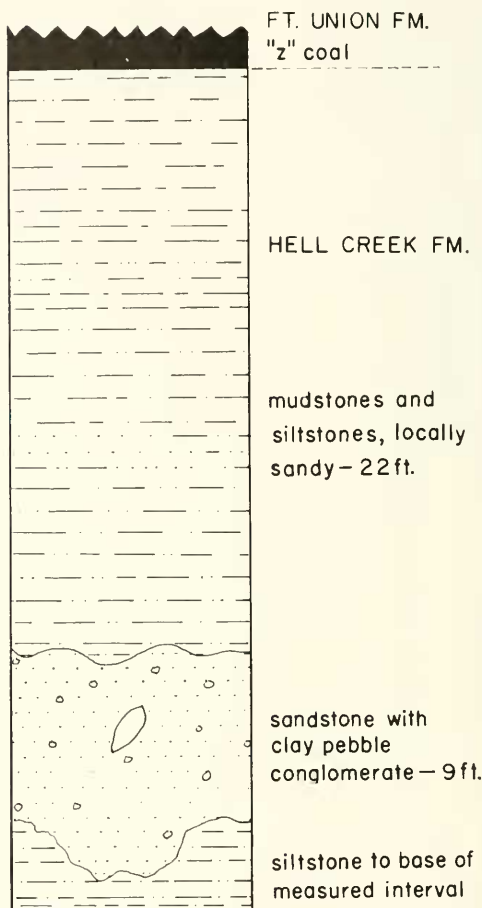

Fig. 2. Geologic section at type locality.

The Hell Creek Formation is Upper Cretaceous (Maestrichtian) in age, its uppermost strata Potassium-Argon dated at roughly 63 million years old (Gill and Cobban, 1973). The vertebrate fossils found with the specimen included scales of ganoid fishes, crocodile teeth and bones, and indeterminate dinosaur fragments. In the older literature, the Hell Creek beds were considered part of the Lance Formation, and Hell Creek specimens were often described as "from the Lance," or "from the Laramie Cretaceous" (e.g., Hay, 1908). Turtles previously known from the

Hell Creek Formation include the following baenid genera (Gaffney, 1972a): *Hayemys, Plesiobaena, Eubaena, Stygiochelys, Palatobaena,* and *Neurankylus.* Trionychids (soft shelled turtles) have been found in the Hell Creek, Lance, and Judith River Formations.

SYSTEMATIC METHODOLOGY

In this study, I name, diagnose, and describe a new taxon and formulate a hypothesis of its phylogenetic relationships.

A phylogenetic hypothesis must take the form of a three-taxon statement of the sort, "taxa A and B share a common ancestor not shared by C." Hennig (1950, 1966) shows that only shared, uniquely-derived characters (synapomorphies) can demonstrate the relative recency of common descent. A phylogenetic hypothesis is tested against alternate hypotheses and is accepted or rejected based upon the relative parsimony of the alternate hypotheses. Relative parsimony is decided by way of (cf. Nelson, 1970): (1) minimum parallel evolution, (2) anatomical and embryological similarity of presumed synapomorphous characters, (3) minimum parallel evolution of complex characters and characters buffered from requirements of similar adaptive modes of the organisms, and (4) minimum reversal of evolutionary trends. Formulation of phylogenetic hypotheses, and testing them using synapomorphous characters, are herein called "Hennigian analysis," instead of "cladistic analysis." Hennigian analysis provides a corroborated hypothesis of the relative recency of common ancestry, which is then used to nest monophyletic taxa into more inclusive monophyletic groups. Hennigian analysis cannot selectively test the several, alternate, geometric arrangements for only two populations (Fig. 3).

Gaffney (1972a) and Tattersall and Eldredge (1977) contend that the geometry of evolution cannot be tested beyond conventional Hennigian analysis, such hypotheses as are presented in Figure 3 being untestable conjectures. Martin and Whetstone (Ms.) argue that the following criteria will objectively test the various geometrical combinations of evolution: 1) except for evolutionary

reversals, which must be assumed to be rare, a direct ancestor must be primitive (plesiomorphic) for every character whereby it differs from daughter populations, 2) a proposed daughter population cannot predate a hypothesized ancestor, 3) a proposed ancestor which postdates or is contemporaneous with a hypothesized daughter population refutes a hypothesis of a single evolutionary lineage without a cladistic event (Fig. 3-1). Despite its geological age, *Emarginachelys* possesses
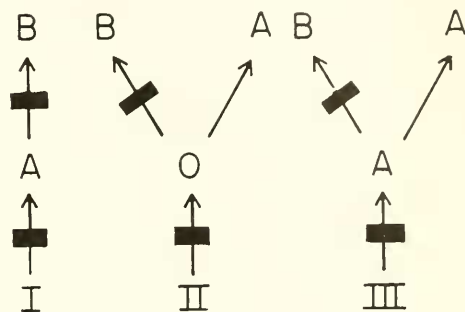

Fig. 3. Alternate hypotheses of phylogenetic linkage between two "taxa." Solid bars represent derived character states. Model II represents the hypothesis that neither "A" nor "B" is ancestral to the other.

many derived features, especially of braincase and plastron, which make unparsimonious any hypothesis of an ancestral position to other known chelydrids.

A thoroughly nested classification presumes coordinate rank of sister taxa. If this concept is used to name each coordinate sister group pair, classifications rapidly become unwieldy and unstable. New names, names of new rank, and a superfluous number of monotypic higher taxa often result (e.g., McKenna, 1975, and Gaffney, 1977). Gaffney (1977), however, argues that "although stability is often considered an important quality of classifications, . . . it is often a spurious and misleading indication of phylogenetic 'truth'." These problems increase markedly with the incorporation of fossil taxa, not because fossil taxa are inherently different, but because many higher taxa must be employed to deal with them.

Patterson and Rosen (1977) suggest a different approach to the classification of

fossils, namely, that "fossil groups or species, sequenced in a classification according to the convention that each group is the (plesiomorph) sister group of all those living and fossil that succeed it, should be called 'plesions.' Plesions may be inserted anywhere (at any level) in a classification without altering the rank or name of any other group. They may bear a categorical name representing any conventional rank, from genus and species upward . . . , these ranks being those already existing in the literature, used only for reference and to avoid ambiguity." I adopt this convention in the classification which follows.

HIGHER PHYLOGENY OF TURTLES

Prior to Gaffney (1975a) most Mesozoic turtles were placed in the "wastebasket" taxon Amphichelydia, thought to be intermediate in structure between living crypotodires and pleurodires. Gaffney presents a convincing shared derived character analysis for a basic crypotodire-pleurodire dichotomy and redistributes most of the taxa previously assigned to the Amphichelydia. The more basic differences between crypotodires and pleurodires are in the trochlear system of the skull for the adductor jaw muscu'ature and the akinetic modifications of the braincase and "palatoquadrate." Cryptodires have a processus trochlearis oticum and a pterygoid brace to the braincase, while pleurodires have a processus trochlearis pterygoidei and a quadrate brace.

Within the Cryptodira, Gaffney recognizes four superfamilies, the Baenoidea, Chelonioidea, Trionychoidea, and the Testudinoidea. In the Trionychoidea he places the kinosternids, dermatemydids, trionychids, and *Carretochelys*, based on the reduction of the stapedial artery and the presence of the "caudifibularis" muscle (Zug, 1971), both assumed to be synapomorphous. Trionychoids also have the costal bones meeting behind the neurals, a reduced postorbital bone, and lack a biconvex 4th cervical vertebra.

If based solely upon the arterial condition and the musculature, a hypothesis of monophyly for these taxa would be questionable. The reduction of the stapedial artery in kinosternids and *Dermatemys* results from enlargement of the palatine artery, while in trionychids and *Carretochelys* it is the result of the enlargement of the pseudopalatine artery (McDowell, 1961; Albrecht, 1967). Neither arterial condition seems intermediate to the other and I suggest that they are nonhomologous. Walker (1973) has interpreted Zug's "caudifibularis" as the dorsal head of the M. flexor tibialis externus that has shifted its insertion from the tibia (the primitive insertion found in most turtles) to the fascia overlying the tibia. This muscle shift is found in all trionychoids, but it is not of such complexity that parallel evolution would be unparsimonious.

Reduced postorbitals are also found in some testudinids and pleurodires but have been acquired independently in these taxa. An elongate (primitive, but often laterally reduced) postorbital is found in all chelydrids, some testudinids (e.g. *Chrysemys scripta*), in most other cryptodires, and in some pleurodires. A reduced neural series is characteristic of most pleurodires but is also assumed to be convergent since some primitive pleurodires have a complete series of neurals (e.g. *Platychelys*). The absence of a biconvex 4th cervical centrum is presumed to be primitive for turtles.

The Chelonioidea as defined by Gaffney (1975a, p. 418, 428) excludes the more primitive members which Gaffney places in this group, the Plesiochelyidae. A more thorough, derived character analysis which attempts to incorporate these turtles is given by Gaffney (1976), who concludes that all chelonioids have a high dorsum sellae, not overhanging the sella turcica as in testudinoids, and which bears a prominent sagittal ridge. An examination of the dorsum sellae of other reptiles reveals that crocodiles, many lizards, some dinosaurs, and *Captorhinus* also have a high, non-overlapping dorsum sellae. DeBeer (1937, p. 256) notes that the dorsum sellae is high in early embryos of *Emys*. This structure even bears a sagittal ridge in *Captorhinus* (see Fox and Bowman, 1966). My initial reaction to these comparisons was to consider the high dorsum sellae of chelo-

nioids as a primitive feature shared by the reptiles cited, but the presence of the low dorsum sellae in baenoids, testudinoids and pleurodires indicates, in the absence of other evidence, that the common ancestor of cryptodires and pleurodires possessed a low dorsum sellae and that the chelonioid structure is a shared, derived character. A discovery that some primitive cryptodires or pleurodires have a high dorsum sellae would refute this hypothesis and support the view that these groups reduced the dorsum sellae independently. Other derived characters in the braincase and forelimbs are shared by the advanced chelonioid taxa, including the Toxochelyidae, to which chelydrids have been allied by some observers (Hay, 1908, p. 27; Zangerl, 1953, p. 267).

The testudinoids form a homogenous group for which I can hypothesize only a single, weak synapomorphy, the biconvex 4th cervical vertebra. Characters which may relate them to other turtles include: 1) the biconvex 4th cervical vertebra—absent in primitive baenoids and "trionychoids," present in all chelonioids in which cervicals are known; 2) loss of mesoplastra—mesoplastra present in baenoids, lost in all other cryptodires; 3) loss of nasal bones—nasals present in primitive baenoids and primitive chelonioids, absent in trionychoids and testudinoids, 4) emargination of temporal region of skull—skull roof well developed in *Proganochelys,* baenoids and chelonioids (except for *Corsochelys*), emarginate in all testudinoids and trionychoids, except *Macroclemys* and *Platysternon.* I suggest that testudinoids and trionychoids form a monophyletic group sharing relatively great temporal emargination and loss of nasal bones, and that their most immediate common ancestor lacked a biconvex 4th cervical. A biconvex 4th cervical is hypothesized to have been independently derived by testudinoids, some baenids and chelonioids. This is not yet a convincing argument, since it is based on characters that seem to be "easily" acquired, but I propose it as a testable hypothesis.

Monophyletic groups within the Testudinoidea may be proposed as shown in figure

4. The Chelydridae, including *Emarginachelys, Chelydra, Protochelydra* and *Macroclemys,* are diagnosed by derived characters as discussed below. Testudinids (*sensu* Romer, 1956) share two, biconvex cervical vertebrae (Williams, 1950), a character not found in other cryptodires, except *Neurankylus* (see Wiman, 1933). Within the Testudinidae, only *Platysternon* and the Emydinae (of McDowell, 1964) have a double articulation between the 5th and 6th cervical centra. The Emydinae are further characterized by the loss of the "batagurine" process and, in more advanced genera, by the reduction of the pterygoid. As a group, the Batagurinae are diagnosed only by primitive characters, although monophyletic complexes occur within the subfamily as defined by McDowell. Advanced testudines share a number of derived characters including: 1) a high, convex shell; 2) alternate constriction and expansion of the costals; 3) thickened epiplastra; 4) expanded coracoid; 5) reduction of phalangeal number; 6) fusion of ventral margins of femoral trochanters; 7) contact of quadrate posterior to incisura collumella auris; 8) depression of the palate in ventral view; 9) ventral processes of the prefrontals far apart (Loveridge and Williams, 1957; Auffenberg, 1974). Many of
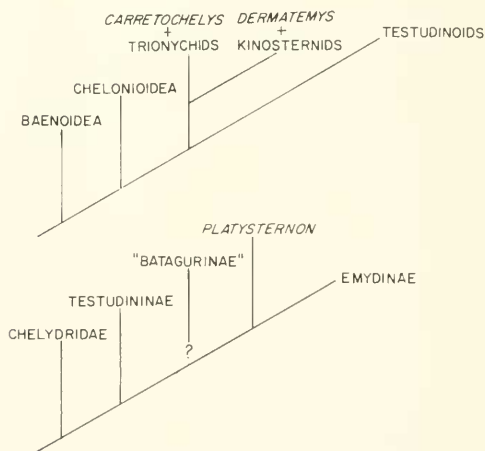

Fig. 4. Hypothesized phylogeny of cryptodiran turtles (top) and testudinoids (below).

these characters are absent in the more primitive living and fossil taxa currently assigned to this group and Auffenberg (1974) suggests that some of the characters may have evolved several times.

In the following discussions, comparisons with baenids and plesiochelyids are based on Gaffney's (1972a, 1976) descriptions and figures unless otherwise noted. Comparisons with *Protochelydra* are based on Erickson's (1973) figures and tables. Terminology of cranial structures follows Parsons and Williams (1961) as illustrated by Gaffney (1972b).

SYSTEMATIC DESCRIPTION

Superfamily TESTUDINOIDEA
Family CHELYDRIDAE
Genus *EMARGINACHELYS* n. gen.

Type species.—*Emarginachelys cretacea* n. sp.

Diagnosis.—Cryptodiran turtle with processus trochlearis oticum and pterygoid brace to the braincase; foramen stapedio-temporale not reduced; nasal bones absent; prefrontals downturned anteriorly; frontals bordering the orbits; the skull roof narrowed above the orbits; otic bridge broad; supraoccipital crest long and low; jugal and postorbital bones elongate; premaxillary "hook" absent; quadrate open behind the stapes; cheek region with some lateral emargination; foramen posterior canalis carotici interni not bordered by basisphenoid; foramen carotico-pharyngeale not enlarged; fossa for attachment of the pterygoideus musculature not extending far anteriorly; triturating surface of maxilla narrow, with a prominent secondary ridge; pterygoid "waist" neither broad, as in *Chelydra,* nor greatly constricted, as in *Macroclemys temminckii;* vomer contacting palatines posteriorly; foramen nervi trigemini and foramen cavernosum small, situated anterior to the dorsum sellae; prootic contacting processus clinoideus laterally; epipterygoid (?) absent; dorsum sellae low, overhanging the sellae turcica; neither foramen caroticum laterale nor foramen anterior canalis carotici interni enlarged; one biconvex cervical ver-

tebra; costal bones not meeting behind the neurals; no serration of the carapace posteriorly; supramarginal scutes absent; carapace weakly keeled medially, costals with parallel ridges; peripherals unsculptured; no carapacial fontanelles; nuchal bone with long, costiform processes; plastron cruciform, ligamentously attached to the carapace; entoplastron reduced, but not "T" shaped; right and left sides of plastron in contact, but not sutured together; thecal process on the ilium; pectineal processes of the pubis not laterally expanded; pubis and ischium separated medially.

EMARGINACHELYS CRETACEA n. sp.

Diagnosis.—Same as for the genus.

Holotype.—KUVP 23488: carapace; plastron; skull lacking lower jaw; right stapes, posterior horn of hyoid; right forelimb and girdle lacking phalanges of digits IV and V; left forelimb and girdle lacking pisiform and distal half of metacarpal V; left hindlimb and girdle lacking most of digits I and V and the distal phalanx of digit IV; right ilium; cervicals 3-7; anterior half of cervical 8; caudals 1-3.

Horizon and Type Locality.—Hell Creek Formation (Upper Cretaceous); Garfield County, Montana; SW ¼ NW ¼ S. 35, T. 21 N., R. 37 E.

MORPHOLOGIC AND COMPARATIVE DESCRIPTION

Skull, Dorsal View (Fig. 5, 6).—The skull roof is composed of the frontal, prefrontal, parietal, and postorbital bones. Nasal bones are absent. The prefrontals are strongly downturned anteriorly, unlike *Chelydra* and *Macroclemys.* The descending process of the prefrontal forms the anterior wall of the fossa orbitalis and the posterior wall of the fossa nasalis. The dorsal portion of the fissura ethmoidalis is not broadly expanded as in testudines or *Adocus,* but resembles the condition in *Chelydra* and emydines. The foramen supraorbitale is preserved on the right side and is indistinguishable from that of *Chelydra.*
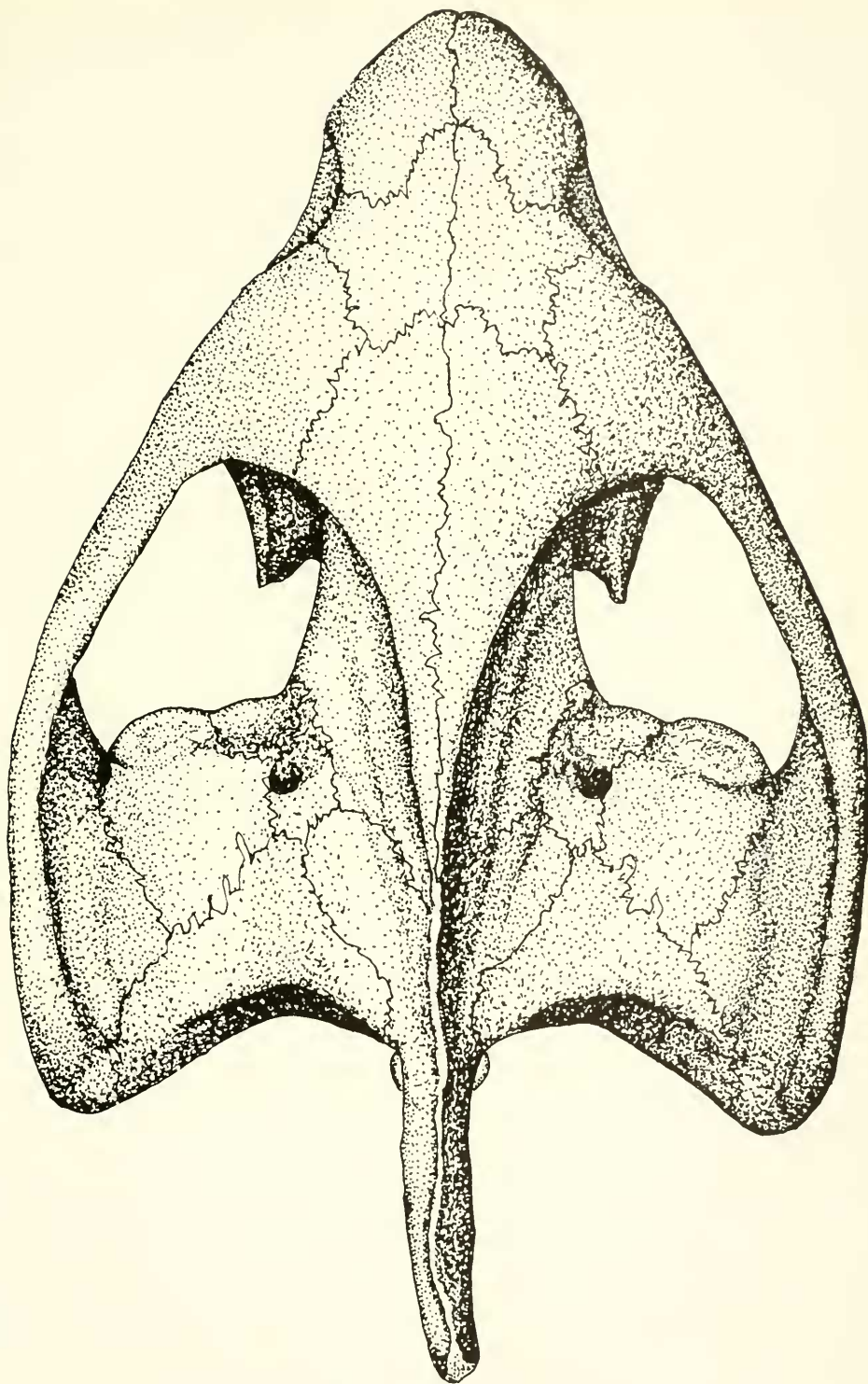
FIG. 5. *Emarginachelys cretacea* (KUVP 23488), restoration of skull in dorsal view. Skull length (condyle to tip of snout) is 77 mm.
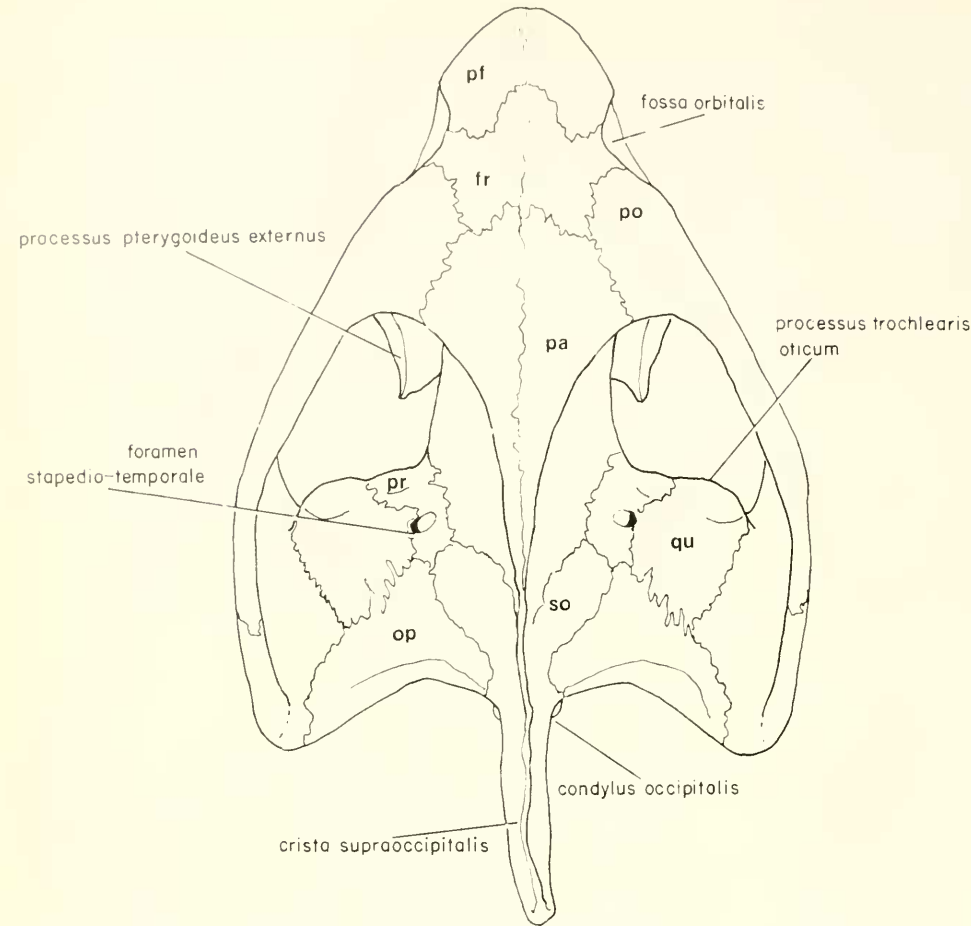
FIG. 6. Key to Figure 5.

TABLE 1: Skull Measurements for Holotypes of *Emarginachelys* and *Protochelydra.*

	Emargi-nachelys	*Proto-chelydra*
Skull length (condyle to tip of snout)	77.1 mm	77.8
Maximum skull width	57.0	69.8±
Width across quadrates ..	52±	68
Width of posterior alveolar surface	10.1	16.5
Width of snout at anterior end of orbit	18.7	20±
Width of snout at posterior end of orbit	31.2	38.2±
Anterior snout height	13.5±	14
Distance from anterior wall of orbit to nasal notch	6.4	6.2
Distance from posterior rim of orbit to anterior margin of temporal emargination	11.4	15.7

The frontals are relatively large and make up a large portion of the skull roof. The prefrontal and postorbital bones do not meet above the orbits. This allows the frontal bones to contact the dorsal margins of the fossa orbitalis. Contact of the frontal bones with the orbits is a primitive feature for cryptodires that is lost in other chelydrids and in some other testudinoids. *Dermatemys* and *Trionyx* have the primitive relationship between the frontal bones and the orbit.

Compared to those of *Chelydra,* the parietals of *Emarginachelys* are much reduced by the extreme posterior emargination of the temporal region. Gaffney (1975b) theorized that such emargination was primitive for the Chelydridae. The fully-roofed condition, is however, almost certainly primi-

tive for the Cryptodira as judged by the temporal regions of baenoids, chelonioids, some pleurodires, and *Proganochelys*. Gaffney's hypothesis is supported by presence of the emarginate condition in the temporal region of the Upper Cretaceous *Emarginachelys,* and I interpret the expanded temporal region of *Macroclemys* as an evolutionary reversal. The skull roof bones of *Emarginachelys* are not strongly sculptured as in *Chelydra*. The frontals extend as far forward on the skull midline as the anterior margin of the orbits. Above and between the orbits, the skull roof is constricted as in *Chelydra* and *Protochelydra*.

The otic bridge, which covers the otic region dorsally, is longer antero-posteriorly than in any other chelydrid or *Platysternon*. In this respect, *Emarginachelys* resembles trionychoids and primitive emydines, and I assume that a broad otic bridge is primitive for testudinoids. The foramen stapediotemporale is situated between the prootic and the quadrate. The sutural contacts between the squamosal, quadrate, and opisthotic bones are partially obscured by cracks, but are interpreted to be as in Figure 6. The supraoccipital crest is long, but is lower than in *Chelydra* or *Macroclemys*.
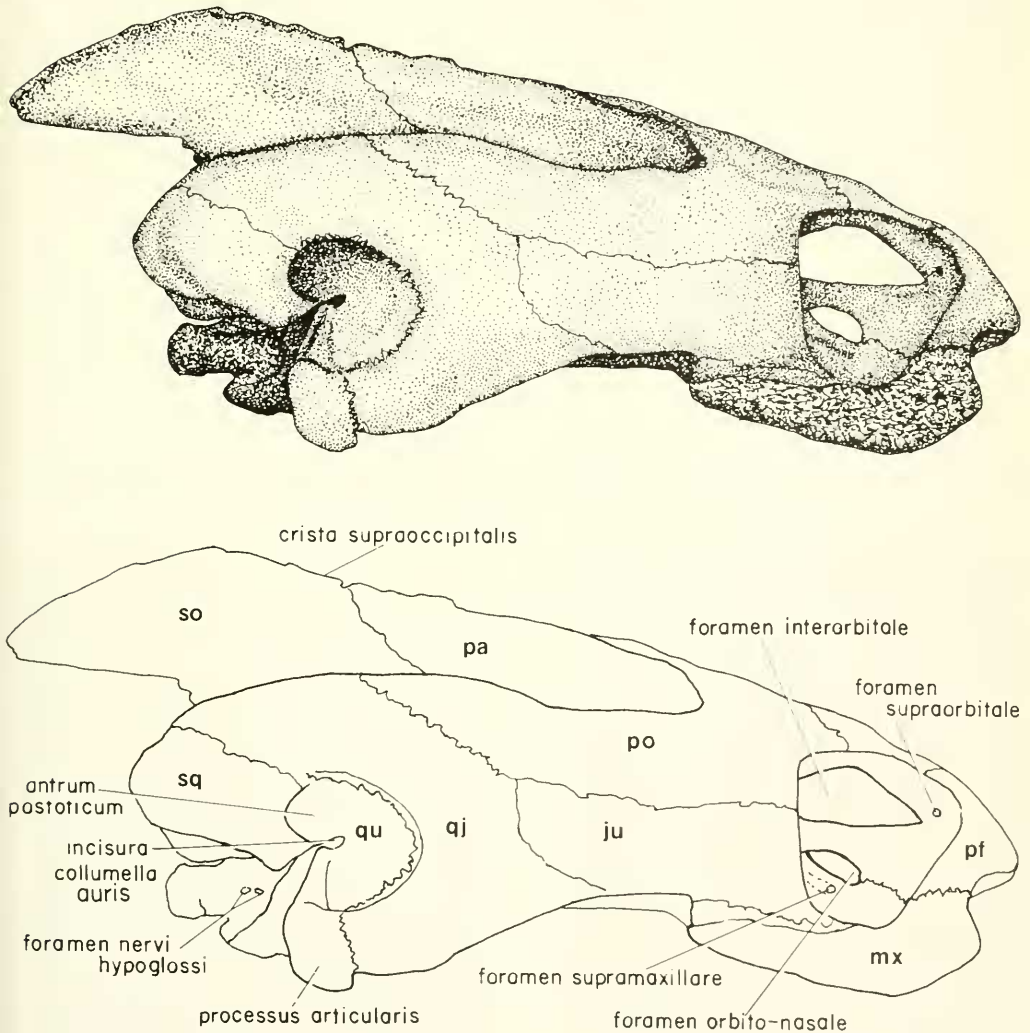

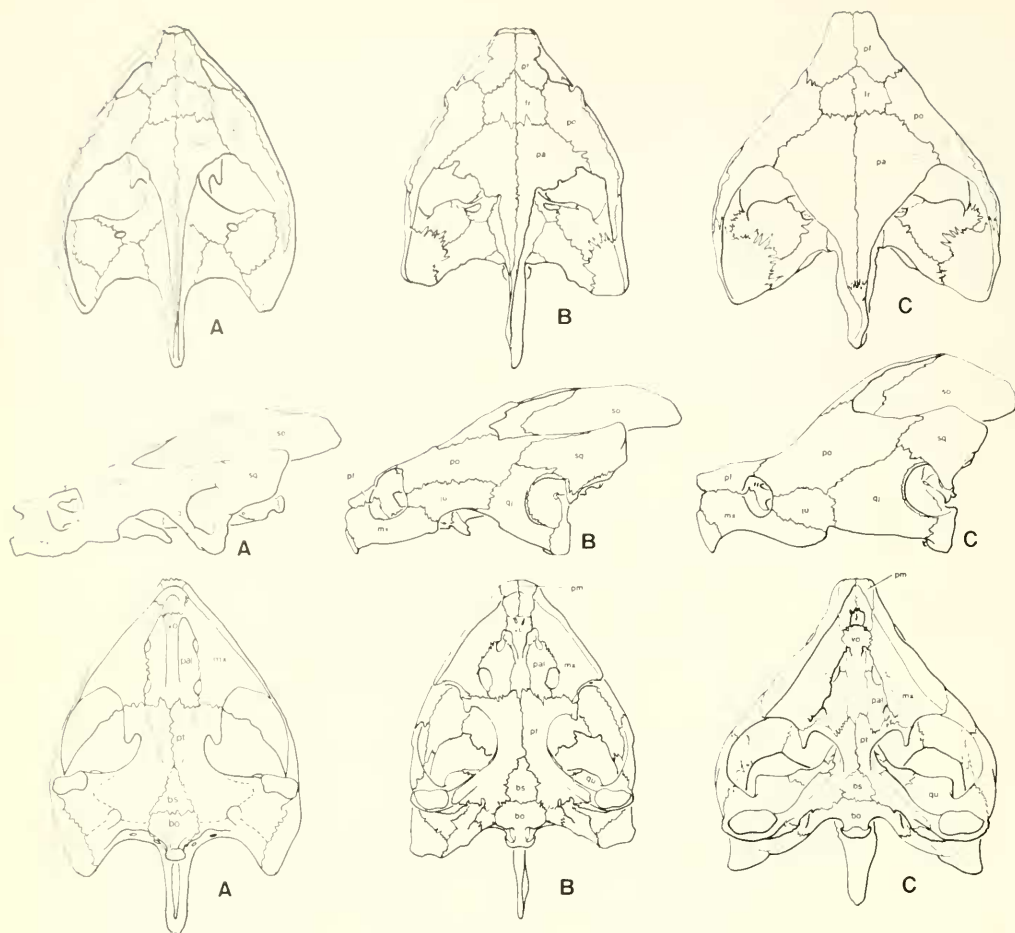FIG. 7, 8. Fig. 7—Restoration of skull in lateral view. Skull length is 77 mm. Fig. 8—Key to Figure 7.

FIG. 9. Skulls of other chelydrid turtles: A) *Protochelydra*, B) *Chelydra*, C) *Macroclemys* (A after Erickson 1973 and Gaffney 1975b; B, C after Gaffney 1975b). Not to scale.

Lateral View (Fig. 7, 8).—The orbital rim is large and prominent, bounded by the prefrontal and maxillary anteriorly and by the jugal and postorbital posteriorly. The infraorbital canal and foramen orbital-nasale are situated approximately as in *Chelydra*. The orbit is partially walled posteriorly by medial extensions of the jugal and maxillary and by a lateral extension of the palatine. A well-developed, posterior wall for the fossa orbitalis is not found in *Chelydra* or *Platysternon*, but is found in some kinosternids and in *Macroclemys*. In *Emarginachelys*, the inframaxillary artery entered this wall anteriorly and exited through the foramen palatinum posterius after passing through a short canal. The foramen palatinum posterius is small, unlike that of *Chelydra*, but

like the foramen of *Macroclemys*.

The premaxillae are not produced into a "hook" as they are in other chelydrids, kinosternids, some testudines, and *Platysternon*. The maxillae are not constricted towards the midline. The jugal and postorbital are relatively long as in all chelydrids. Gaffney (1975b) hypothesized that a relatively long jugal was primitive for the Chelydridae. This hypothesis was based on the presence of a long jugal in the geologically old *Protochelydra* (Fig. 9), since almost all cryptodires have relatively short jugals. The presence of a long jugal in *Emarginachelys* does support this hypothesis, even though this bone is substantially shorter than in *Protochelydra*. The shorter jugal in *Macroclemys temminckii* is interpreted as a

reversal. The postorbital bone is long in chelonioids, baenoids, and chelydrids and this condition is probably primitive for cryptodires. In the "cheek" region, *Emarginachelys* is only slightly emarginate, unlike *Protochelydra* and *Chelydra,* but similar to *Macroclemys.* This does not support Gaffney's (1975b) hypothesis of a primitively emarginate cheek region for chelydrids. The weakly emarginate condition also occurs in the primitive baenoids, *Trinitichelys* and *Naomichelys,* and in *Platysternon, Damonia, Proganochelys, Desmatochelys* and chelonids. I suggest that the relatively-great, lateral emargination of *Chelydra* and *Protochelydra* may be a shared, derived feature for these turtles.

The incisura columella auris of the quadrate is narrowly open posteriorly, unlike the quadrates of all other chelydrids and most testudines. The open condition is probably primitive, since it occurs in most cryptodires (including emydines), and in most sauropsid reptiles. The processus articularis of the quadrate is much shorter in *Emarginachelys* than in *Chelydra.*

Ventral View (Fig. 10, 11).—The tuberculum basioccipitale is accentuated by the strong depression of the basioccipital to accommodate the insertion of the rectus capitis muscle. There is little postero-lateral expansion of the pterygoid, leaving the otic region more open ventrally than in other chelydrids or *Dermatemys.* The processus interfenestralis and the prootic are exposed ventrally in the fenestra postotica. The ventral margin of the foramen posterior canalis carotici interni is formed by the pterygoid; the dorsal margin by the prootic.

The right stapes is preserved more or less in place. The footplate of the stapes is flattened and the shaft does not extend from the center of the footplate. Both plesiochelyids and other chelydrids have a similar stapedial morphology, a condition which I interpret as primitive. *Dermatemys* and kinosternids have conical footplates that are symmetrical about the shaft of the stapedial rod (McDowell, 1961), an additional synapomorphy uniting these taxa.

The ventral surface of the basisphenoid extends only slightly beyond the mandibular condyles anteriorly, as in *Protochelydra* and some emydines. *Macroclemys, Chelydra,* baenids and plesiochelyids generally have the basisphenoid extending farther beyond the mandibular condyles. I am uncertain which condition is primitive for testudinoids. On the pterygoid brace to the braincase, lateral to the basisphenoid and posterior to the fossa temporalis inferior, are depressions for the attachment of the pterygoideus musculature like that of many emydines (e.g. *Graptemys*), *Macroclemys,* baenids, and plesiochelyids. I suggest that a posterior depression for the pterygoideus musculature is primitive and that the extension of the depressed surface anterior to the area of the processus pterygoideus externus is a derived character shared by *Chelydra* and *Protochelydra* (see Erickson's figure 1).

The skull of *Emarginachelys* is narrower in many proportions than is that of *Chelydra* (compare Figs. 9 and 10). The distance between the quadrates is relatively less, as is the width of the pterygoid waist, the distance between the processi pterygoidei externi, and the distance between the postero-medial margins of the triturating surfaces of the upper jaws. The processi pterygoidei externi of *Emarginachelys* are only slightly extended ventrally. The triturating surfaces of the maxillae are relatively narrow and bear a pronounced median ridge on the posterior portion, similar to that of some testudinids. Among cryptodires, this type of ridging is found only in some testudinids *(sensu lato),* *Dermatemys,* and *Adocus,* and seems to be correlated with herbivory. Since ridging is lacking in kinosternids and trionychids, which share a number of derived characters with *Dermatemys,* the presence of midline maxillary ridges cannot be used to unite *Emarginachelys* with dermatemydids.

The foramen palatinum posterius is small, unlike this foramen in *Chelydra.* It is situated near the postero-medial corner of the maxilla. The labial ridge of the maxilla is straight, unserrated and prominently raised from the level of the triturating surface. The labial ridge is continued across the midline by the premaxillary bone. There is no premaxillary "hook," a derived feature shared by other chelydrids, and no median recess
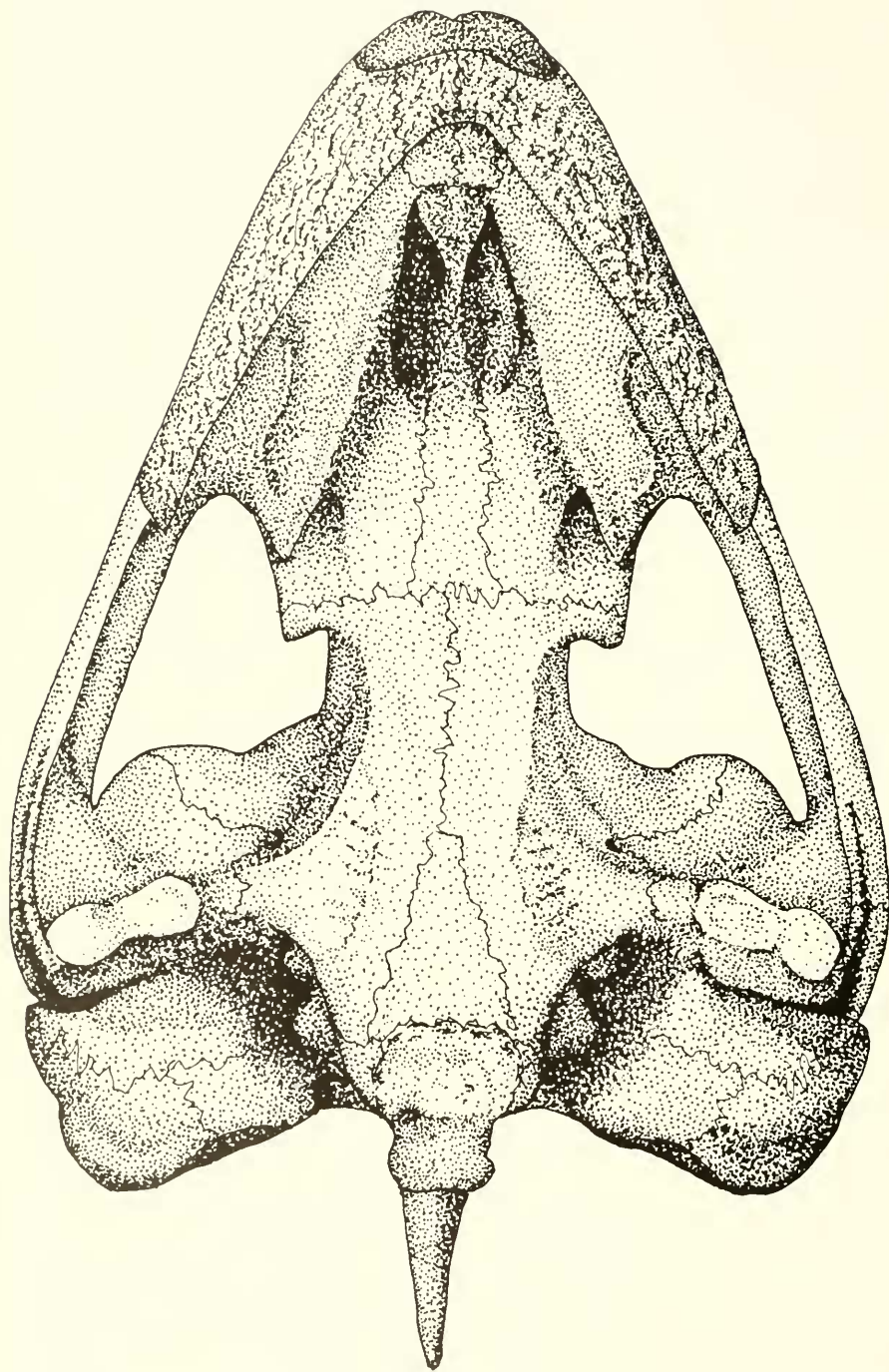
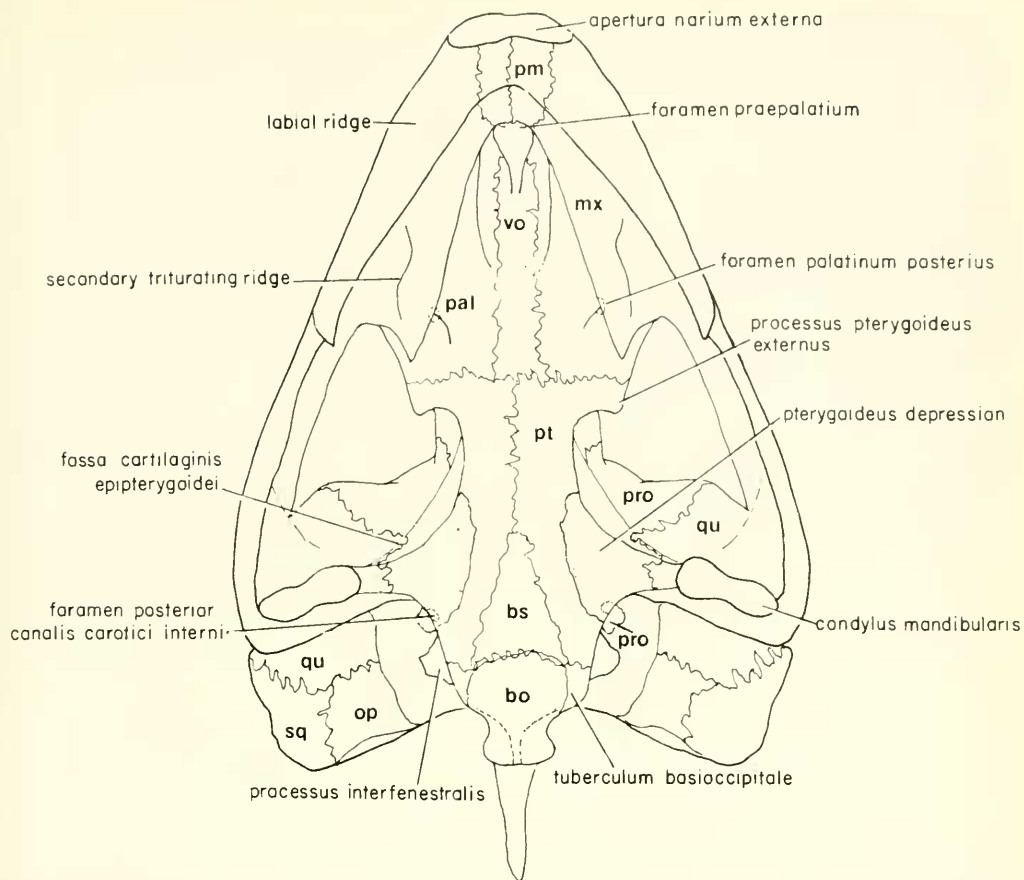Fig. 10. Restoration of skull in ventral view. Same scale as Figure 5.

FIG. 11. Key to Figure 10.

exists in the premaxillary. A median recess is present on premaxillae of emydines and batagurines. The triturating surface of the maxilla narrows anteriorly and terminates at the sutural contact between the vomer and the maxilla. The vomer and premaxillae bear the paired foramina praepalatina. As in all chelydrids, the vomer contacts the palatines posteriorly and is not crested ventrally.

Braincase (Fig. 12).—The parietals form most of the side wall of the braincase. The foramen nervi trigemini is small and is situated dorsal and anterior to the dorsum sellae. Its margins are formed mostly by the prootic internally and mostly by the parietal externally. There is a distinct fossa cartilaginis epipterygoidei, but there appears to be no independently ossified epipterygoid. It is also possible that I have incorrectly interpreted, as cracks, the sutures which delimit this bone. The quadrate is narrowly excluded

from the foramen nervi trigemini, but forms the posterior border of the fossa cartilaginis epipterygoidei. The descending processes of the parietals are broad. In this respect and in the dorsal position of the foramen nervi trigemini, *Emarginachelys* resembles *Dermatemys* and is unlike *Chelydra* and *Macroclemys*.

The structure of the floor of the braincase is difficult to interpret, due to both its uniqueness and to post-mortem damage. The left side of the braincase anterior to the dorsum sellae is considerably crushed and the right side posterior to the dorsum sellae has been damaged by root growth into the skull. The foramen cavernosum is situated anterior to the dorsum sellae, just ventral to the trigeminal foramen. The anterior placement of the foramen cavernosum is, to my knowledge, unique among turtles. The situation is apparently the result of the union of the
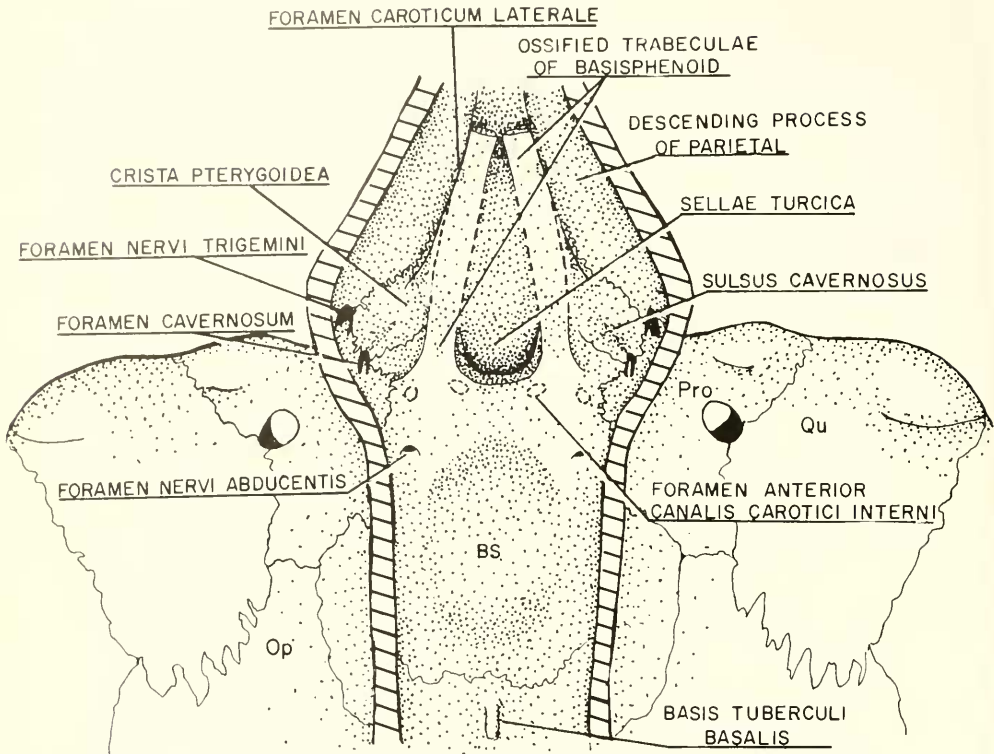
FIG. 12. Restoration of braincase in dorsal view.

processus clinoideus with the prootic which is anteriorly expanded medial and dorsal to the area normally occupied by the sulcus cavernosus. The dorsum sellae is low and overlaps the floor of the sellae turcica. The anterior internal carotid foramina are situated beneath the shelf of the dorsum sellae and are closer together than in *Chelydra*. Part of the trabecula of the right side is preserved; beneath it the lateral carotid foramina can be located with probes. They are close in size to the anterior internal carotid foramina, but direct measurement is impossible. The crista pterygoidei is short and bears the sulcus cavernosus as it rises toward the foramen cavernosum.

Cervical Vertebrae.—Most of the third through eighth cervical vertebrae are preserved. The cervical, central articulations may be represented by Walther's (1922) formula as (3(4)5)6 7 8. This is comparable to the cervical central pattern of *Macroclemys* and *Chelydra*. With only rare

exceptions, these turtles have the patterns (2(3(4)5)6)7)8) and (2(3(4)5)6 7 8) (Williams, 1950). The eighth cervical of *Emarginachelys* is not biconvex as in emydines, batagurines, testudines, and *Platysternon*. A biconvex, fourth cervical is a derived character which occurs only in some eucryptodires (sensu Gaffney), with the possible exception of *Neurankylus*. The cervical centra of *Emarginachelys* are much shorter than those of recent chelydrids with a comparably sized carapace. Otherwise the centra are morphologically similar to those of *Chelydra* and *Macroclemys*.

Carapace and Plastron (Fig. 13).—The carapace and plastron of *Emarginachelys* shows features absent in other chelydrids. The bones of the carapace are thick, especially the neurals and peripherals. There is no emargination anteriorly and scalloping posteriorly. There are 11 pairs of peripherals, 8 pairs of costals, 8 neurals, 2 suprapygals, and one nuchal. The neurals are longer than
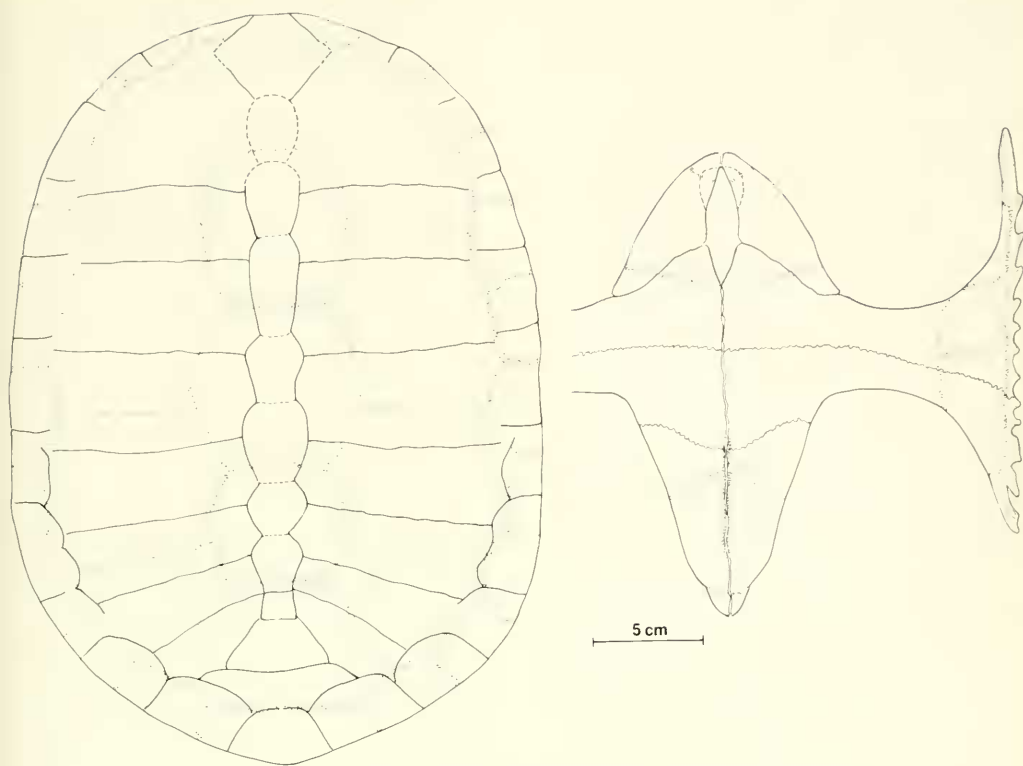
Fig. 13. Partial restoration of carapace and plastron.

wide and narrow sharply anteriorly. The impression of the most anterior vertebral scute cannot be discerned. The impressions of the remaining vertebrals are about as wide as they are long and approximately square in outline. There are no supramarginal scutes as are found in *Macroclemys temminckii*.

A low, median keel extends from the 4th neural posteriorly to the base of the posterior suprapygal. Auxillary ridges extend from the posterior of the 4th through 7th neurals and diverge anteriorly and laterally, terminating after a short distance. Costals 5 and 6, on the inferior half, and costals 4 and 5, on the superior half, are strongly sculptured with parallel ridges similar to the costal sculpture of *Pseudemys*. Costals with similar sculpture from the Upper Cretaceous Lance Formation were described by Estes (1964). These may belong to *Emarginachelys*, rather than to *Neurankylus* as suggested by Gaffney (1972a). There is no sculpture on the peripherals. Cross sections of several periph-

erals are shown in Figure 14. Peripherals 4, 5 and 6 are elongated in the ventral direction for the attachment of the plastron. There is a lateral "keel" on these peripherals that merges on peripherals 3 and 7 with the ventral margin of the carapace. Pits in the ventromedial margins of the peripherals are directed inward and downward for reception of the digitate lateral projections of the plastron. The 4th and 7th peripherals are the more deeply pitted while the 5th and 6th are shallowly pitted at the ventro-medial margin. The posterior peripherals are tapered as in *Dermatemys*.

The broad prezygapophyses of the first dorsal vertebra curve downward and outward to allow vertical flexure of the neck. The ventral surfaces of the succeeding dorsal vertebrae are not flattened as in *Chelydra*. The 2nd, 3rd, and 4th dorsals are ventrally keeled as in *Dermatemys*, but the more posterior dorsals are ventrally rounded. The 9th and 10th dorsals are procoelous, the 10th

strongly so. The ribs of the 10th dorsal are free. Ribs of the three sacral vertebrae are modified for a support for the pelvic girdle, as in *Chelydra*. The distal rib-heads of the costals fit into "V" shaped notches in the peripherals. There appears to have been no ventral closure of the peripherals under the distal rib ends. There are no fontanelles between the costal and peripheral plates as occurs in other chelydrids and in some toxochelyids.

The plastron is cruciform, with broad antero-posterior extensions of the hyo- and hypoplastra for the ligamentous attachment with the carapace. A ligamentously attached "buttress" extends from the antero-lateral prong of the hyoplastron along the medial margin of the peripherals and attaches in a pit at the juncture of the 3rd and 4th peripherals, the point of termination of the costiform process of the nuchal bone. The anterior margin of the carapace is thus braced by a ring of bone extending anteriorly from the right 4th peripheral across the anterior margin to the left 4th peripheral. I am not sure of the functional advantages of such a bony support, but I suspect that it is associated with the reduced, ligamentously attached plastron in a heavy bodied, semi-aquatic turtle.

The entoplastron is not "T" shaped as in other chelydrids, but is roughly triangular in outline, with a narrowly tapered posterior tip. It is articulated to the surrounding plastral bones by a kinetic squamous articulation (Fig. 13). Some of the anterior portion of the entoplastron extends laterally over the dorsal surface of the epiplastra and is not visible in ventral view (Fig. 13). The hyo- and hypoplastra are strongly sutured together with most of the plastral bridge being formed by the hyoplastron. The epiplastra are broad compared to those of other chelydrids. The epiplastra articulate with the hyoplastra by convexo-concave "joints" and the right and left epiplastra do not suture together at the midline. The remaining plastral elements articulate with their counterparts of the other side in a loose kinetic articulation. This plastral morphology is unique and highly derived, differing from that of sea turtles. Plastral kinesis allowed free movement of

the plastron by flexure perpendicular to the antero-posterior axis. The strong sutures between the hyo- and hypoplastra allowed no kinesis at the midline perpendicular to a lateral axis.

The impressions of the three inframarginal scutes and the gular, humeral, and anal scutes are preserved. They are essentially as in *Macroclemys*. Impressions of the remaining plastral scutes cannot be determined.

Analysis of Shell Morphology.—The shell of *Emarginachelys* differs from that of other chelydrids in the absence of plastral and carapacial fontanelles. In this respect it resembles most adult testudinids (sensu Romer), dermatemydids, baenids, some kinosternids and some *Plesiochelys* (Bram, 1965). I interpret shell reduction by fontanellization as a shared, derived feature for *Protochelydra* (lacks plastral fontanelles), *Chelydra,* and *Macroclemys*. The *Emarginachelys* entoplastron and xiphiplastra are reduced, relative to the primitive condition of cryptodires, but not as reduced as in *Chelydra* and *Macroclemys*. I interpret the "T" shaped entoplastron, reduced epiplastra, and serrated carapacial margin as further synapomorphies uniting *Protochelydra, Chelydra* and *Macroclemys* and the further reduction of the xiphiplastra as derived features shared by *Macroclemys* and *Chelydra*. If *Protochelydra* and *Chelydra* share a common ancestor not shared by *Macroclemys,* as suggested here, then reduced xiphiplastra and plastral fontanelles would be hypothesized to be derived in parallel.

The cruciform plastron and long costiform processes on the nuchal bone are also found in kinosternids and are particularly well developed in *Staurotypus*. These features, plus the presence of a single, biconvex cervical vertebra, were used by Williams (1950, whose classification was followed by Romer, 1956) to unite chelydrids and kinosternids into a single family. Since these features are absent in *Dermatemys,* which shares a derived cranial artery pattern with kinosternids (McDowell, 1961; Albrecht, 1967; Gaffney, 1975a), I suggest that the costiform process and the cruciform plastron were independently derived in kinosternids and chelydrids. The 4th cervical is biconvex in chelydrids while other cervicals are bioconvex in kinosternids and *Dermatemys*.
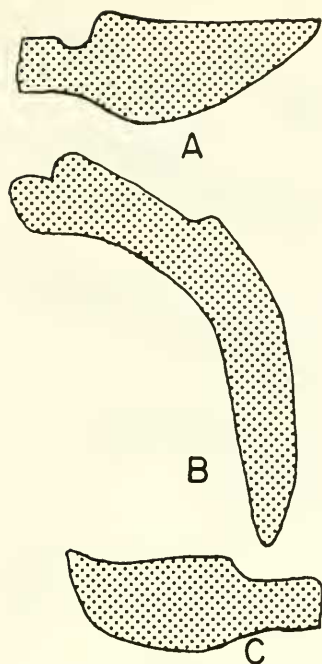
FIG. 14. Semi-diagrammatic cross sections of peripheral bones: A) 9th right, B) 5th right, C) 2nd right. Natural size.

Plastral "buttresses," extensions of the plastron which suturally contact the costals, occur in many pleurodires, baenoids, dermatemydids, and testudinids and are assumed to be primitive for cryptodires. If the long, anterior extensions of the hyoplasta of *Emarginachelys* represent a reduced buttress, then the complete loss of a buttress would be a synapomorphy uniting other chelydrids. Ligamentous attachment of the plastron to the carapace is a derived feature found in all chelydrids, some emydines, *Platysternon,* and *Claudius* among non-chelonioid cryptodires. Since sutural attachment, the plesiomorphous condition, occurs in most testudinids (sensu lato), *Dermatemys,* and kinosternids, I regard ligamentous plastral attachment as examples of parallelism for chelydrids and these other taxa.

Shell morphology has been used (e.g. Hay, 1908; Zangerl, 1953) to suggest a close relationship for chelydrids and toxochelyids. These taxa share the cruciform plastron, "T" shaped entoplastron, ligamentous attachment of carapace to plastron, costo-peripheral fon-

tanelles, and plastral fontanelles, all derived characters for cryptodires. Gaffney (1975a, 1976) suggests that this shell reduction is convergent.

The toxochelyid braincase indicates clearly the affinities of toxochelyids with the plesiochelyids and other chelonioids, as proposed by Gaffney. Derived features of the *Toxochelys* braincase which are shared by some, or all, of the chelonioids, but not by chelydrids, include: 1) a high, crested dorsum sellae that does not overlap the sella turcica (see discussion above); 2) approximated internal carotid arteries; 3) fusion of the ossified trabeculae with reduction of the sellae turcica. The taenia intertrabecularis (see Nick, 1912) may be present as a keel atop fused trabeculae of toxochelyids (Whetstone and Stewart, Ms.). The shell morphology of *Emarginachelys,* which I regard as the most primitive chelydrid, supports Gaffney's hypothesis of convergent shell reduction for chelydrids and toxochelyids, since *Emarginachelys* lacks most of the shell reduction found in later chelydrids or in toxochelyids.

Pectoral Appendages (Fig. 15, 16).—The left and right forelimbs are preserved essentially as they were articulated in life. The left forefoot lacks only the pisiform bone and the proximal half of the fifth metacarpal. Except for the structure of the intermedium, the morphology of the forelimb compares closely with that of adult chelydrids—the metatarsals and phalanges are relatively short and broad; the phalangeal formula is 2-3-3-3-3; the centralia are fused. The intermedium is wedge shaped, extending medially onto the distal surface of the *radius* (Fig. 15). To my knowledge, this carpal morphology is unique to *Emarginachelys.*

The humerus is similar to that of *Chelydra.* It is strongly "S" shaped, with the neck extending outward from the distal part of the shaft at an angle (angle "alpha" of Zangerl, 1953) of about 90 degrees. Its head is elliptical, with a prominent, lateral shoulder. The humeral shoulder of *Chelydra* and *Protochelydra* is poorly-defined while that of *Macroclemys* and *Emarginachelys* is prominent. There is a well-defined, intertrochanteric fossa immediately behind the head. The shaft of the humerus is massive, unlike the slender
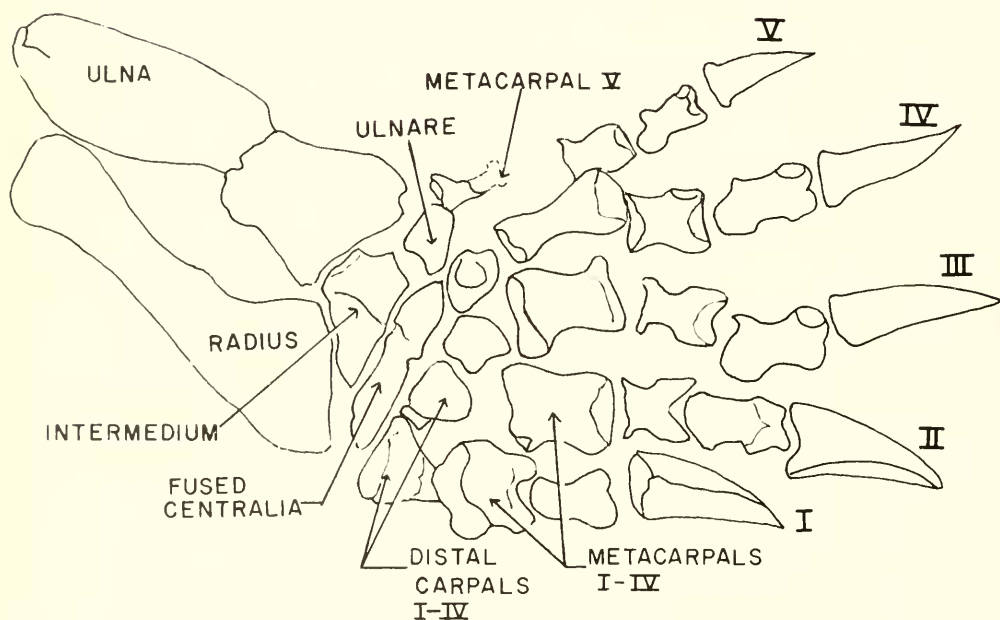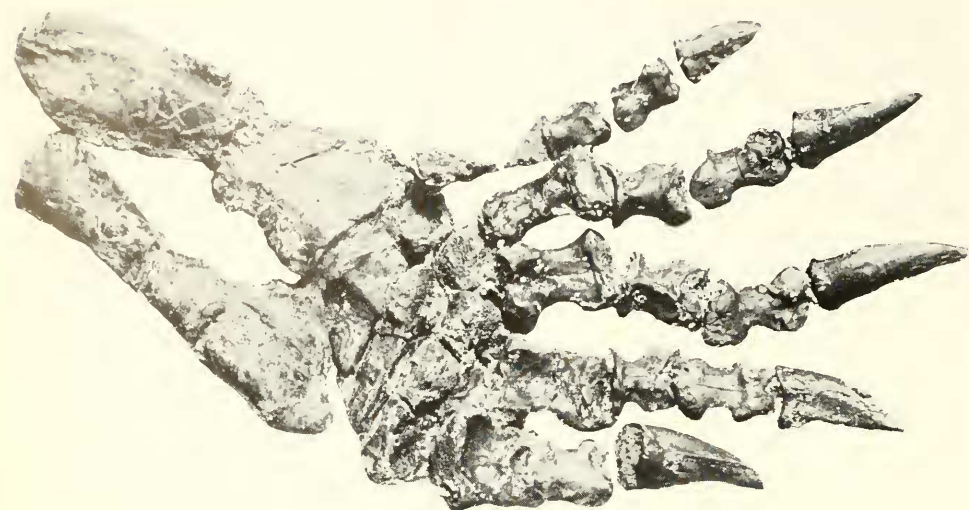
Fig. 15. Left forefoot, radius and ulna. Natural size.

humeri of emydines and *Platysternon*. Distally the shaft expands and bears two stout condyles.

Pectoral Girdle (Fig. 17)—As in all living turtles, the pectoral girdle is a three-pronged structure with postero-medial, medial and dorsal processes. The pectoral girdle compares closely with chelydrids except that the coracoid is less expanded than in *Chelydra,* and the ventro-medial process of the scapula is more massive.

Pelvic Appendages (Fig. 15, 18).—The left

Fig. 16. Left—Lateral and dorsal aspect of left humerus; Right—Ventral and dorsal aspect of left femur. Natural size.

hind limb and the left half of the pelvic girdle are well preserved. The left foot lacks most of digits I and V. As far as can be determined, the phalangeal formula is the same as in *Chelydra*. Of the tarsals, the astragalus and calcaneus are fused; a bump on the distal edge of the astragalus probably represents the fused centrale. The astragalus, calcaneus, and centrale are usually well fused in adult chelydrids, but are sometimes discernible or separate in juveniles (cf. Zug, 1971).

The femur is similar in size and general morphology to that of *Chelydra*. The femoral trochanters are more massive than those of *Chelydra*, with constriction of the intertrochanteric fossa. The fossa is partially enclosed ventrally by a low ridge which connects the distal borders of the trochanters. There is much greater curvature in the shaft than in *Macroclemys* or *Chelydra*. The distal con-

dyles are strongly produced from the ventral surface.

Pelvic Girdle (Fig. 19).—The ilium is strongly inclined posteriorly; at the dorsal end it expands into a rugose surface which served for ligamentous attachment of the pelvis to the carapace. There is a well-developed, thecal process on the anterior margin. Among living cryptodires studied by Zug (1971), only kinosternids have the thecal process on the ilium. If the presence of this process is considered synapomorphous, *Emarginachelys* might be presumed to share a common ancestor with kinosternids and *Dermatemys* that is not shared by chelydrids. I do not accept this interpretation. As discussed above, the cranial circulation of *Dermatemys* and kinosternids is unique and presumably synapomorphous. If a close relationship with *Emarginachelys* exists, the *Dermatemys* ossified shell and the
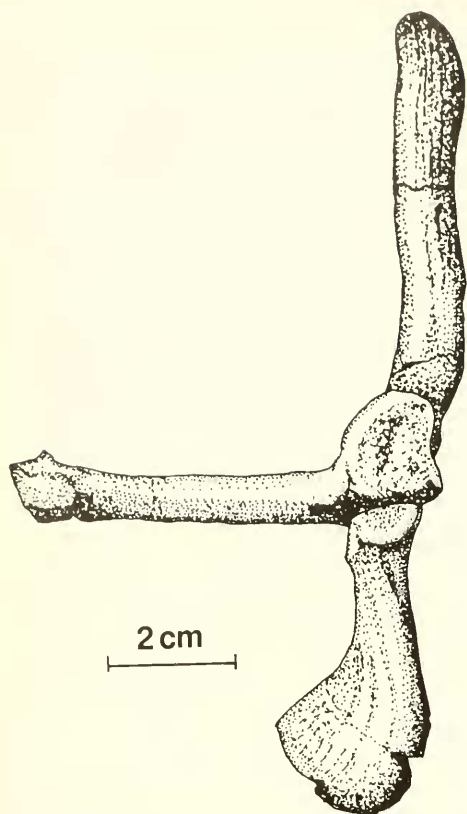
2 cm

FIG. 17. Left scapulocoracoid in anterior and slightly
ventral view.

ilium without a thecal process would be
hypothesized as evolutionary reversals, or the
reduced plastron and ligamentous plastral
attachment of *Emarginachelys* would be
hypothesized as convergence with chelydrids.
Emarginachelys also has the costals not meet-
ing behind the neurals, a biconvex 4th cervi-
cal, an elongate jugal, and non-divergent
pectineal processes (see below). I prefer to
regard the thecal process as independently
acquired for kinosternids and *Emargin-
achelys*. A similar process occurs on ilia of
some *Toxochelys* and of *Chisternon,* a baenid.

The pubis is narrower medially than in
Chelydra. It is notched antero-medially for
the insertion of the epipubic cartilage. Antero-
laterally the pubis bears a process, the pec-
tineal process, which was attached to the
plastron by ligaments. Zug (1961) shows
that only *Macroclemys* and *Chelydra* among
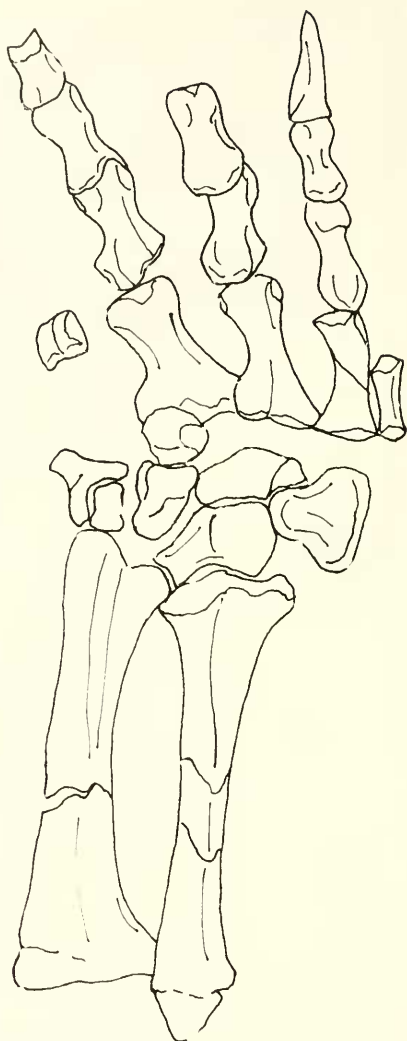living cryptodires have the pectineal process

FIG. 18. Left hindfoot, tibia, and fibula. Natural size.

parallel to each other and to the sagittal plane
(Fig. 20). I interpret this as a synapomorphy
for advanced chelydrids. The pubis of *Proto-
chelydra* is not known. The *Emarginachelys*
pelvis is intermediate between other crypto-
dires and chelydrids in having the pectineal
processes neither broadly divergent nor par-
allel.

In most testudinids, including *Platysternon,*
the medial surfaces of the ischium and pubis
are approximated, usually with a diamond-
shaped foramen between the two bones (Fig.
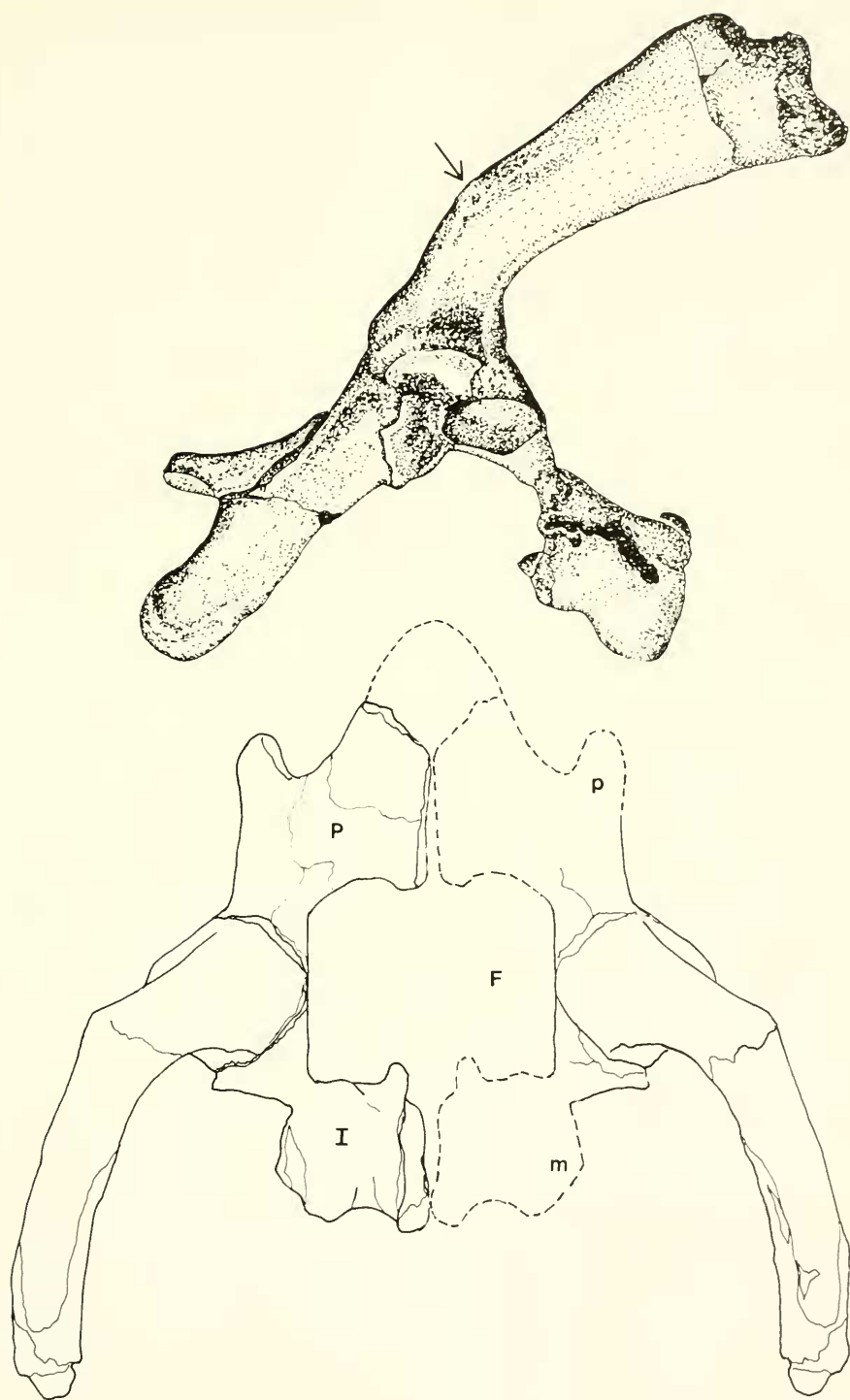20). The pubis of living chelydrids (and

Fig. 19. Above—Left half of pelvis in lateral view. Note thecal process at arrow. Below—Partial restoration of pelvic girdle in dorsal view. Abbreviations as in Figure 20. Natural size.
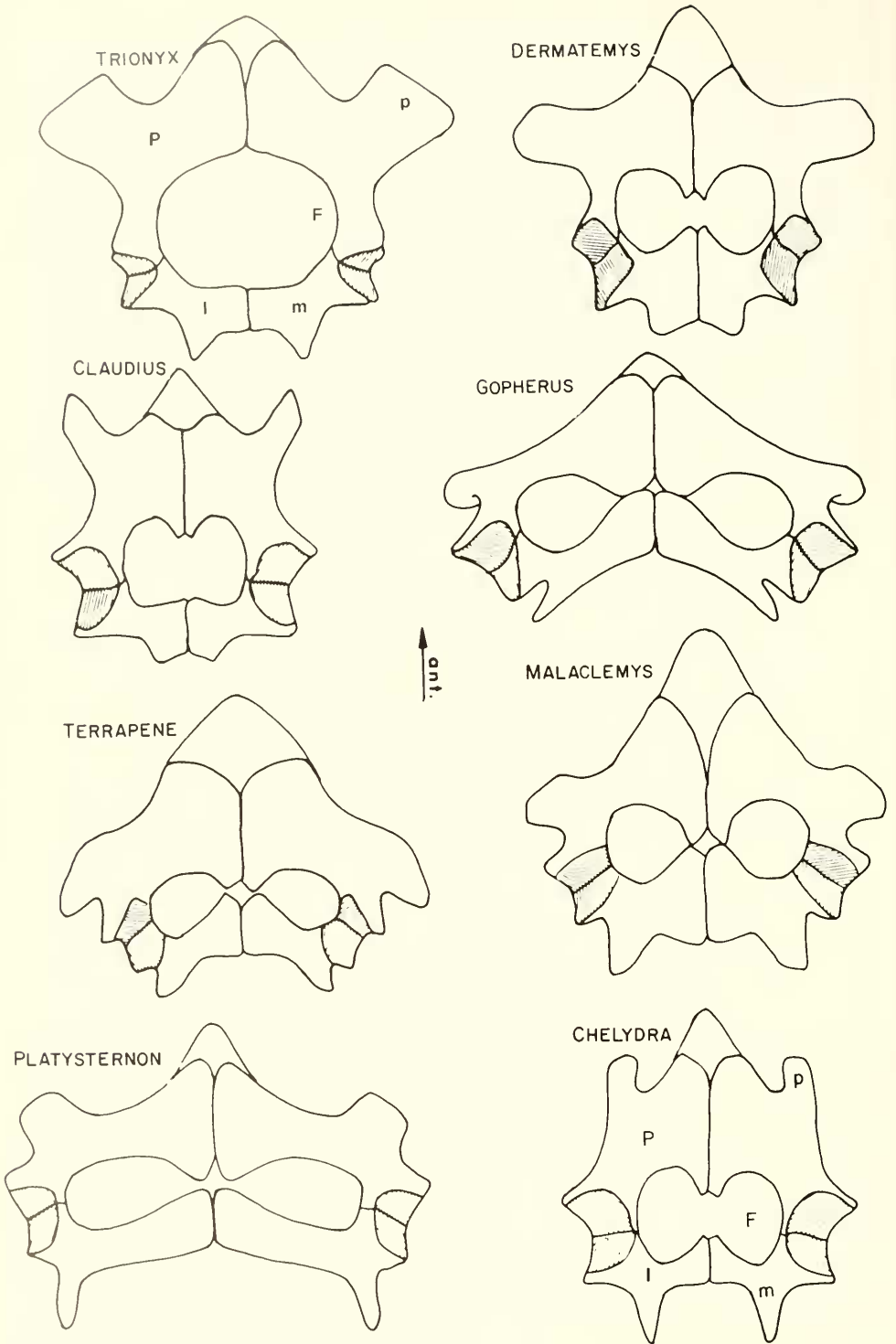
FIG. 20. Pelvic girdles of some cryptodiran turtles in dorsal view, after Zug (1971). Abbreviations: P- pubis, p- pectineal process of pubis, F- puboischiadic foramen, l- ischium, m- metischial process.
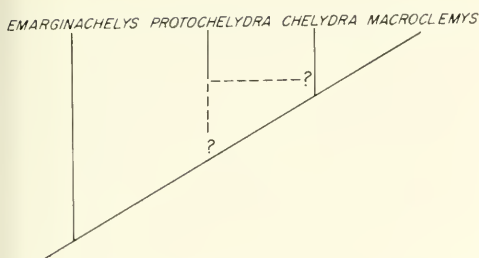
EMARGINACHELYS PROTOCHELYDRA CHELYDRA MACROCLEMYS

Fig. 21.   Alternate hypotheses of the relationships of chelydrid turtles.

Emarginachelys) is relatively widely separated from the ischium, although the cartilage connecting them may calcify late in life. There is no diamond-shaped foramen in living chelydrids or *Emarginachelys*. In *Emarginachelys* there is a ventrally-directed, metischial process not present in *Chelydra* or *Macroclemys*.

PHYLOGENY AND CLASSIFICATION OF CHELYDRID TURTLES

The four genera of chelydrid turtles recognized here (*Emarginachelys, Protochelydra, Chelydra,* and *Macroclemys*) are hypothesized to be a monophyletic group sharing the following derived characters: 1) a cruciform plastron with reduced entoplastron, 2) a long costiform process on the nuchal bone, 3) ligamentous attachment of the plastron to the carapace, 4) an elongate jugal bone, and 5) the pectineal processes of the pubis not broadly divergent. The separation of the abdominal scutes may also be a synapomorphous character, but the impressions of these scutes are not known for *Emarginachelys*. Characters (1) and (3) are also found in toxochelyids and *Claudius*, and character (2) in kinosternids. This distribution is assumed to be the result of convergence since the sister groups of kinosternids and toxochelyids have the primitive condition of these characters.

Protochelydra, Chelydra, and *Macroclemys* are hypothesized to share a common ancestor not shared by *Emarginachelys*, since they share peripheral fontanelles, a closed quadrate, serrated carapacial margin, frontals not bordering the orbits, constriction of the otic

bridge, less emarginate skull roof, and formation of a bony "beak" by the premaxillary bone. Parallel pectineal processes may also be synapomorphous at this level. Gaffney (1975b) proposes a unique common ancestor for *Macroclemys* and *Chelydra*. This hypothesis is supported by the presence of plastral fontanelles, reduced xiphiplastra, and a less emarginate temporal region in these genera. An alternate hypothesis is that *Protochelydra* and *Chelydra* share a unique, common ancestry. This hypothesis is supported by the great lateral emargination of the cheek region and the extension of the depression for the pterygoideus musculature anterior to the region of the processus pterygoideus externus. I accept Gaffney's more parsimonious hypothesis and this phylogeny is reflected by the classification which follows.

Gaffney (1975b) placed the Asiatic genus *Platysternon* in the Chelydridae, on the basis of a presumed sister-group relationship to *Macroclemys*. Study of additional specimens of the Miocene *Macroclemys schmidti* indicate that some of the characters assumed by Gaffney to be synapomorphies actually represent convergences (Whetstone, 1978). Also, *Platysternon* lacks the cruciform plastron, narrow epiplastra, "T" shaped entoplastron, serrated carapacial margin, a long costiform process on the nuchal bone, separated abdominal scutes, and parallel pectineal processes of the pubis which are found in *Chelydra* and *Macroclemys*. If *Platysternon* shares a common ancestor with *Macroclemys* not shared by *Chelydra*, these lost characters must be interpreted as evolutionary reversals. *Platysternon* shares at least one presumed synapomorphy with testudinids, as discussed above, and an additional synapomorphy with emydines alone.

A CLASSIFICATION OF CHELYRID TURTLES

Family CHELYDRIDAE Swainson, 1839
  Plesion EMARGINACHELYS New Name
  Subfamily Chelydrinae Swainson, 1839
    Genus *Protochelydra* Erickson, 1973
    Genus *Macroclemys* Gray, 1855
    Genus *Chelydra* Schweigger, 1812

ACKNOWLEDGEMENTS

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